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Quantitative Genetic Application in the Selection Process for Livestock Production

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Additional information is available at the end of the chapter

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1. Introduction

Quantitative genetic analysis is performed on traits showing a continuous range of values, such as height and weight. However, traits displaying a discrete number of values (such as number of offspring) and even binary traits (such as disease presence or absence) are all amenable to quantitative genetic analysis. The genetic architecture of a complex trait consists of all the genetic and environmental factors that affect the trait, along with the magnitude of their individual effects and interaction effects among the factors. The quantitative genetics approach has diverse applications. It is fundamental to an understanding of the variation and co-variation among relatives in natural and managed populations, of the dynamics of evolutionary change, and of the methods for animal improvement and alleviation of complex disease. The roots of quantitative genetics trace back to the work of Galton and Pearson in 1880–1900, who developed many of the basic statistical tools (such as regression and correlation) used in quantitative genetics. Indeed, many of the basic statistical tools now commonly in use were first introduced and developed in the context of quantitative genetics. A major principle of animal breeding is to select those animals to become parents that will improve the genetic level in the next generation. For quantitative traits that are unable to observe the genotype, it can only measure the phenotypic value, which is influenced both by genotype and by environment. Therefore, it needs a way to infer the breeding value from the phenotypic value in such a way to maximize the probability of choosing the correct animals to become parents. The purpose of animal breeding is not to genetically improve individual animals, but to improve animal populations. To improve populations, basic tools are required to identify and utilize genetic differences between animals for the traits of interest. In animal breeding, knowledge of the genetic properties of the traits that are interested in is the first prerequisite in establishing a selection program. This chapter will try to define and explain the factors that influence animal's genetic progress during the selection process.

2. Genetic parameters for selecting process

Most of the economic characters in farm animals that are of concerning to a breeder normally show continuous variation. There is a wide range of variability in these characters which depends on the genetic which make up of the individuals and the environment in which they are grown. For breeding plans, it is necessary to know the relative significant of the heritable and environmental variation of the characters. Breeders use this variability for getting improvement in economic characters through efficient selection strategies. Designing of effective selective breeding programs requires quantitative information concerning nature and scale of genetic and environmental sources of variation and correlation for components of performance. The information on genetic parameters, such as heritability, repeatability, and genetic correlation is a prerequisite for making efficient selection strategies by the geneticists and breeders. In animal breeding, reliable estimates of the genetic variance, environmental variance, and their ratios are important in providing information about the mechanism of inheritance of phenotypically observed characteristics in animals, estimating breeding values, and designing and optimizing breeding programs.

2.1. Values and variance components

When working with a quantifiable phenotypic trait, the measurement taken for a specific individual will be its phenotypic value (P). This value can be broken down into two main components: the portion that is a result of the individual genotype (G) and the portion that is due to environmental conditions (E).

$$P(\text{phenotypic value}) = G(\text{genotype value}) + E(\text{environmental deviation})$$

The genotypic value can be divided in three main components that contribute to the genotypic value. Breeding value (A), Dominance deviation (D) due to deviation of the heterozygote from the average of the two homozygote and Interaction or Epistasis (I) due to interaction among non-allelic genes.

$$P = A + D + I + E$$

The breeding value (A) is a measure of how much an individual's genetic make up contributes to the phenotypic value of the next generation. The breeding value is a calculation determined by the gene frequencies in a population for a given locus, and a measure called the average effect. When considering an allele, we would like to know how much that single allele, if found in an offspring, will change the trait measure of that individual away from the population mean. This is called the average effect.

When analyzing the phenotypic values of a trait within a population, comparisons are made using variance and the phenotypic variance is divided between various components.

$$V_P = V_A + V_D + V_I + V_E \quad (1)$$

V_P = Phenotypic Variance

V_A = Additive Genetic Variance

$V_D + V_I$ = Non-Additive Genetic Variance

V_E = Environmental Variance

Genotypes or genotypic values are not passed on from parents to progeny; rather, it is the alleles at the loci that influence the traits that are passed on. Therefore, to predict the average genotypic value of progeny and their predicted average phenotype, investigators need to know the effect of alleles in the population rather than the effect of a genotype. The effect of a particular allele on a trait depends on the allele's frequency in the population and the effect of each genotype that includes the allele. This is sometimes termed the average effect of an allele. The additive genetic value of an individual, called the breeding value, is the sum of the average effects of all the alleles the individual carries [7].

2.2. Additive genetic variance

The additive variance is the variance of breeding values. It is the chief cause of resemblance between relatives and therefore the major determinant of the observable genetic properties of the population and of the response of the population to selection. How do geneticists estimate additive genetic variance? Two methods are generally used; parent-offspring regressions and analysis of variance. The first case can be illustrated by assuming that we have milk records on a number of dam-daughter pairs. We then compute the regression of the daughter on her dam. The following equation can be described:

$$b_{op} = \frac{\sigma_{op}}{\sigma_p^2} \quad (2)$$

Where b_{op} is the regression of offspring on her dam, σ_{op} is the parent-offspring covariance, and σ_p^2 is the phenotypic variance, as defined above. Assuming that there are no sources of similarity between daughters and dams except for additive genetic variance, then σ_{op} will be equal to one half of σ_A^2 , since a parent passes one half of its genome to its progeny. Thus σ_A^2 can be estimated as follows:

$$\sigma_A^2 = 2b_{op} \sigma_p^2 \quad (3)$$

For example assume that σ_p^2 for annual milk production equal 1,000,000 kg, and $b_{op} = 0.12$. Then $\sigma_A^2 = 240,000$ kg.

To estimate σ_A^2 by analysis of variance, assume that we have a population consisting of a number of sires, each with a relatively large number of daughters. Assume further that each sire was mated to a random sample of dams, and that all environmental effects are randomly distributed. If these conditions are true, we can then assume that the between-sire component of variance from an ANOVA (abbreviation: Analysis of Variance) will consist only of additive genetic effects.

2.3. Heritability

Heritability is the single most important consideration in determining appropriate animal evaluation methods, selection methods and mating systems. Heritability measures the relative importance of hereditary and environmental influences on the development of a specific quantitative trait. Broad-sense heritability, defined as $h^2 = V_G/V_P$, captures the proportion of phenotypic variation due to genetic values that may include effects due to dominance and epistasis. On the other hand, narrow-sense heritability, $h^2 = V_A/V_P$, captures only that proportion of genetic variation that is due to additive genetic values (V_A). Note that often, no distinction is made between broad and narrow sense heritability; however, narrow-sense h^2 is most important in animal and plant selection programs, because response to artificial (and natural) selection depends on additive genetic variance. Moreover, resemblance between relatives is mostly driven by additive genetic variance [12].

The numerical value of a heritability estimate can be increased or decreased by changing its component parts. An increase results from a reduction in the environmental variance or from an increase in genetic variance. Conversely, a decrease results from an increase in environmental variance or from a decrease in genetic variance. Heritability measurement varies from zero to one. Heritability close to one indicates that all the variability among individuals is only attributable to additive genetic effect of genes. Conversely, while a small heritability implies that V_A is small, it tells us little about V_G , as genetic effects could be largely in non-additive terms (V_D and V_I). Thus, a character h^2 can still have very considerable genetic variation at loci contributing to the observed character variation. A trait with heritability value of zero suggests that all the phenotypic variation among individuals in the population is due to environmental and non-additive genetic effects. Hence, ($V_A = 0$) does not imply that the character lacks a genetic basis; it implies only that the observed trait variation within the population being considered is entirely environmental.

Traits with heritabilities in low group include those related to fertility, such as lambing, calving, and foaling percentage; litter size in swine, dogs and cats; and hatchability in chickens. Milk production and growth traits measured at weaning are two examples of traits with medium estimates of heritability. Highly heritable traits include those measured in animals when they are more mature, such as feedlot traits, carcass traits, and yearling and mature weights.

Heritability tells the breeder how much confidence to place in the phenotypic performance of an animal when choosing parents of the next generation. For highly heritable traits where h^2 exceeds 0.40, the animal's phenotype is a good indicator of genetic merit or breeding value. For lowly heritable traits, where h^2 is below 0.15, an animal's performance is much less useful in identifying the individuals with the best genes for the trait.

Heritability can tell us how closely genetic merit follows phenotypic performance, but it tells us nothing about the economic value of better performance. Some traits with low heritabilities, such as the survival and fitness traits, have low heritabilities but high economic value. Other traits, like stature, are moderately to highly heritable, but have

insufficient economic value to be given much emphasis in selection programs. Producers should select to improve traits with low heritabilities when economic circumstances justify the attention. In addition, lowly heritable traits of substantial economic value should always be targeted for improvement through better environmental conditions. Traits of low heritability can be selected for successfully by using aids to selection such as progeny testing and multiple records on individual animals. Standardized environmental conditions can actually increase heritability by reducing the non-genetic differences between animals. Modern milking facilities, large herds, better nutrition, and skilled management personnel have all increased the opportunity for genetic improvement of health, reproductive, and fitness traits. In practice, heritability for economic characters rarely exceeds 0.50, with low values around 0.10 for fertility and prolificacy. The general pattern for h^2 for various traits is strikingly similar across species.

2.3.1. Importance of heritability estimates

Heritability is used to calculate genetic evaluations, to predict response to selection, and to help producers decide if it is more efficient to improve traits through management or through selection and making many practical decisions in breeding methods to predict the animal's estimated breeding value (EBV). By regarding heritability as the regression of breeding value on phenotypic value, an individual's EBV is simply calculated as the product of heritability and the phenotypic value.

Heritability is one important component of the equation used to predict genetic progress from selection to improve a trait. For the simplest form of selection called "mass selection" or selection on phenotypes measured on individuals in a population, that equation is:

$$\Delta G = ih^2\sigma_p \quad (4)$$

If any of these three parts were low, genetic progress through selection would be slow. The economic value of the trait may still justify efforts to improve it through selection; as such, improvement is a permanent change that benefits all future offspring. Heritability helps the producers decide which traits justify improvement through selection.

You can use heritability estimates to estimate progress and setbacks in different traits that you can expect from different mating. For example, a particular mating may bring improvement in rate of gain if the parents are genetically superior. If they are inferior, however, they may cause a decline in rate of gain in their offspring. To illustrate how to figure expected progress from particular mating, assume you have a herd with an average daily gain in the feedlot of 2.40 pounds per day. From that herd, you kept bulls that gained 3.20 pounds and heifers that gained 2.80 pounds per day for breeding purposes. How much gain in genetic improvement could you expect in the progeny of these selected parents? To answer this question, first calculate just how superior these parents were to the average in the herd.

Calculate the superiority of the breeding animals as follows:

- Superiority of dams = 2.80 - 2.40 or 0.40 pounds per day.
- Superiority of sires = 3.20 - 2.40 or 0.80 pounds per day.
- Superiority of parents = (0.40 + 0.80) ÷ 2 = 0.60 pounds per day.

The next question is, "How much of this 0.60 pound advantage is transmitted to the offspring?" To answer, you must know the heritability of feedlot average daily gain. The average estimate for this trait is 0.34. Expected genetic gain, then, is equal to the average superiority of the parents multiplied by the heritability (i.e., 0.60 x 0.34 or 0.20 pounds per day). The herd average was 2.40 pounds feedlot gain per day. With all other things equal, you would expect the offspring of the selected parents to gain an average of 2.40 + 0.20 = 2.60 pounds per day. This is the average of the herd plus the genetic advantage transmitted by the parents. The calculations above illustrate two important points: First, if the selected parents had not been superior in rate of gain over the average of the herd, there would have been no genetic improvement in rate of gain of their offspring, regardless of the degree of heritability of the trait. Second, the amount of genetic progress is also dependent on how highly heritable a trait is. Though the parents had an advantage over the herd average of 0.60 pounds per day in gain, they would not have transmitted any of this advantage to their offspring if the trait had herd heritability. The general conclusion, then, is that the greater the superiority of the individuals selected for breeding purposes and the higher the heritability of the trait, the more progress will be made in selection. The magnitude of heritability dictates the choice of selection method and breeding system. High heritability estimates indicate that additive gene action is more important for that trait, and selective breeding i.e. mating of the best to the best should produce more desirable progeny. Low estimates, on the other hand, indicate that probably non-additive gene action such as dominance and epistasis is important.

Heritability, also, gives a measure of the accuracy with which the selection for a genotype can be made from a phenotype of the individual or a group of individuals. In individual selection, in which members of the population are selected on the basis of their phenotypic values, the accuracy of selection measured in terms of the correlation between genetic values (breeding values), and phenotypic values, r_{AP} , is related to the heritability as follows:

$$r_{AP} = \frac{Cov(A, P)}{\sigma_A \sigma_P} \quad (5)$$

Splitting the phenotypic value as $P = A + R$, where R consist of environmental, dominance and epistatic deviations, and noting that A and R are uncorrelated, then, $Cov(A, P) = \sigma_A^2$. Hence; $r_{AP} = h$. Thus, the square-root of the heritability expresses the reliability of the phenotypic value as a guide to the breeding value.

Another important function of heritability is its role in predicting the breeding value of an individual as well as in predicting the genetic improvement expected as a result of the adoption of particular scheme of selection. For example, assuming linear relationship between breeding and phenotypic values, the best estimate of an individual's breeding value is:

$$\hat{A} = b_{AP}.P \quad (6)$$

Which b_{AP} is the regression of breeding value on phenotypic value. Since, $Cov(A, P) = \sigma_A^2$ and $b_{AP} = h^2$ then:

$$\hat{A} = h^2.P \quad (7)$$

Thus, the best estimation of an individual's breeding value is the product of its phenotypic value and the heritability.

Knowledge of the heritability is sufficient to predict the response to a single generation of selection. Defining the response (R) as the change in mean over one generation, and the selection differential (SD) as the difference between the mean of selected parents and the population mean before selection, it follows from the below equation:

$$R = h^2.SD \quad (8)$$

This is often referred to as the Breeders' equation. If heritability is close to zero, the population will show very little response to selection, no matter how strong the selection. For example, suppose the average value of a character in the population is 100, but only individuals with large values are allowed to reproduce, so that among the reproducing adults the average trait value is 120. This gives $S=120-100=20$, and an expected mean in the next generation of $100 + 20h^2$. If $h^2 = 0.5$, the mean increases by 10, while if $h^2 = 0.05$ the mean increases by only one. The response of selection equation implies that the response to selection depends on only a part of the total genetic variation, namely V_A . The reason for this is that parents pass on single alleles, rather than whole genotypes, to their offspring. Only the average effects of alleles influence the response: any dominance contributions due to interaction between alleles in a parent are not passed on to the next generation, as only a single parental allele is passed to its offspring.

2.3.2. Heritability estimation

Estimation of heritability in populations depends on the partitioning of observed variation into components that reflect unobserved genetic and environmental factors. In other words, researchers recognize that genetic and/or environmental variation exists, but they may not be in a position to assess either directly. However, this does not prevent them from being able to estimate the relative effects of both genes and environment on phenotype. Here, heritability can be estimated from empirical data on the observed and expected resemblance between relatives. The expected resemblance between relatives depends on assumptions regarding a trait's underlying environmental and genetic causes.

Heritability can be estimated in several ways, which will describe the common methods as follows:

1. Regression estimates based on the degree of resemblance between relatives

Resemblance for single traits is evaluated by the use of linear regression. Thus, the heritability (or repeatability) estimator is expressed by the linear regression coefficient [13].

In general, each estimate of heritability is based on the degree of resemblance among related individuals vs. non-related individuals in some animal population. Family units most often used to evaluate degree of resemblance include parent and offspring; parents and offspring; full sibs (i.e., full brothers and/or sisters); and paternal half sibs (i.e., half brothers and/or sisters). Heritability can be derived from estimates of either a regression coefficient or an intra-class correlation among related individuals. The co-variances, regression coefficient, correlation coefficient, and estimates of heritability based on these coefficients for some important relatives are presented in the table (1) below:

Relatives	Covariance (ignoring epistatic)	Regression (b) Intra-class correlation (t)	Heritability Estimate
Offspring and one parent	$\frac{1}{2}V_A$	$b_{OP} = \frac{1}{2}h^2$	$\hat{h}^2 = 2\hat{b}_{OP}$
Offspring and mid- parent	$\frac{1}{2}V_A$	$b_{OP} = h^2$	$\hat{h}^2 = 2\hat{b}_{OP}$
Half-sib	$\frac{1}{4}V_A$	$t_{HS} = \frac{1}{4}h^2$	$\hat{h}^2 = 4\hat{t}_{FS}$
Full-sib	$\frac{1}{2}V_A + \frac{1}{4}V_D + V_E$	$t_{FS} \geq \frac{1}{2}h^2$	$\hat{h}^2 = 2\hat{t}_{FS}$

Table 1. The co-variances, regression coefficient, correlation coefficient, and estimates of heritability based on some important relatives.

In order to decide which sort of relatives are better than those other is, there are mainly two points to consider sampling error and environmental sources of covariance. The statistical precision of the estimate depends on the environmental design and on the magnitude of heritability being estimated and so, no hard and fast rule can be made. The question of environmental sources of covariance is generally more important than the statistical precision of the estimate because it may introduce a bias that can not be overcome by statistical procedure. From considerations of the biology of the character and the experimental design, we have to decide which covariance is least likely to be augmented by an environmental component. The half-sib correlation and the regression of offspring on sire are the most reliable from this point of view. The regression of offspring on dam is sometimes liable to give too high estimation because of maternal effects. The full-sib correlation, which is the only relationship for that an environmental component of covariance is shown in the table, is the least reliable of all. The component of environment due to common environmental cause such as maternal effect is often present in large amount and is difficult to overcome by experimental design and the full-sib covariance is further augmented by the dominance variance. The full-sib correlation can, therefore, seldom more than set an upper limit to the heritability.

2. Selection experiment

Another direct approach for heritability can be estimated from the results of selection experiments. In selective breeding of plants and animals, the expected response to selection can be estimated by the following equation:

$$R = h^2.S \quad (9)$$

In this equation, the Response to Selection (R) is defined as the realized average difference between the parent generation and the next generation. The Selection Differential (S) is defined as the average difference between the parent generation and the selected parents. If R and S are known, then h^2 can be estimated as the ratio R/S , which is known as the realized heritability.

3. Isogenic lines

A simple method of estimating heritability in the broad sense is provided by data on isogenic lines such as identical trials, clones, long inbred lines. In highly inbred population or in crosses between such populations, practically all the variation ought to be due to environmental influences since the individuals have the same genotypes. In the other words, isogenic lines are those lines within which there are no genetic variation and can be analyzed to obtain the estimate of intra-class correlation within lines. If t is the intra-class correlation within lines, then t itself is an estimate of heritability in the broad sense. The estimate is subject to inflation because of any environmental correlation between members of an isogenic line. The method is useful only in the case of identical twins in livestock. As you can follow the equation below:

$$\hat{h}_{(b)}^2 = \hat{t} \quad (10)$$

4. Animal model using restricted maximum likelihood (REML)

Traditionally, heritabilities have been estimated by correlations of close kin, e.g. parent-offspring regressions. During the last decade, the study of evolutionary quantitative genetics in wild populations has made a transition from the traditional use of close-kin comparisons to the more powerful 'animal model' using restricted maximum likelihood (REML) to estimate quantitative genetic parameters in natural populations. An animal model takes into account all relationships in a pedigree and is therefore expected to provide estimates of quantitative genetic parameters with higher precision than estimates restricted to the similarity between close kin. It is also less likely to be biased by complicating factors such as assortative mating, inbreeding, selection, and shared environment.

One of the major recent changes in the study of the quantitative genetics of natural populations has been the use of mixed models, in particular the form of mixed model known as the 'animal model', for the estimation of variance components [15]. In contrast to simpler techniques typically used to estimate heritabilities in studies of wild populations to date, such as parent-offspring regression or sib analyses, these models incorporate

multigenerational information from complex pedigrees and allow estimation of a range of causal components of variance. Furthermore, they are not bound by assumptions of no assortative mating, inbreeding, or selection, and allow for unbalanced datasets.

The animal model is a form of mixed model, the term used to describe linear regressions in which the explanatory terms are a mixture of both ‘fixed’ and ‘random’ effects. Fixed effects are unknown constants that affect the mean of a distribution. Random effects are used to describe factors with multiple levels sampled from a population of possible values, for which the analysis provides an estimate of the variance of the effects rather than a parameter for each factor level. Random effects therefore influence the variance of the trait. In the case of an animal model, the random effects of interest are the additive genetic value of individual animals. For the simplest form of animal model, the phenotype y of individual i is written as:

$$y_i = \mu + a_i + e_i \quad (11)$$

Where μ is the population mean, a_i is the additive genetic merit of individual i , and e_i is a random residual error; the model has no fixed effects other than μ . The terminology “animal model” arises simply because the model is defined at the level of the individual animal. The random effects a_i are defined as having variance equal to σ_A^2 , the additive genetic variance, the residual errors will have variance σ_R^2 and for the simplest animal model equation the total phenotypic variance in y will be $\sigma_A^2 + \sigma_R^2$. Variance components are estimated directly by fitting the respective random effects in a linear model framework, rather than through indirect interpretation from the covariance between relatives. There are two stages to the analysis of an animal model: estimating the variance components and predicting the additive genetic effects (and any other random effects).

2.4. Repeatability

The concept of repeatability enters into accuracy calculations when more than one record is available on an individual. Repeatability measures the degree of association between records on the same animal for traits expressed more than once in an individual’s life. Traits that may be measured more than once include number born, litter weight, and number weaned.

When more than one measurement of the trait can be taken on each individual, the phenotypic variance can be partitioned into variance between and within individuals. The between-individual variance is composed of the genetic variance, σ_G^2 , and a permanent environmental variance, σ_{EP}^2 , while the within-individual variance is expressed by the temporary environmental variance, σ_{ET}^2 . The repeatability is then expressed by:

$$r = \frac{\sigma_G^2 + \sigma_{EP}^2}{\sigma_P^2} \quad (12)$$

The repeatability expresses the proportion of the variance of a single measurement that is due to genetic and specific environmental effects, effects that are then expected to be

repeated in equal strength in repeated measurements. Assumptions when estimating repeatability are 1) equal variances in the different measurements, and 2) different measurements reflect what the same trait genetically is. In a breeding program, the advantage of repeated measurements is seen from the gain in accuracy in breeding evaluation. The phenotypic variance is reduced when σ_{ET}^2 is minimized, and the additive genetic variance increases in proportion to phenotypic variance.

By definition, repeatability must be greater than or equal to heritability for a given trait. Permanent environmental effects do not affect the genetic merit of an individual but do influence the performance and, therefore, all records on an individual. For repeatable traits, observing the performance of an individual several times increases the accuracy of the estimated breeding value compared to an estimate based on a single observation. If more than one record is collected, the number of records, heritability, and repeatability influences the accuracy. The increase in accuracy depends upon the ratio of repeatability to heritability. The reason that accuracy increases less when repeatability is higher is that the higher repeatability means that the similarity between observations is due to non-transmittable effects, permanent environment, and non-additive genetic factors.

2.5. Correlations and genetic correlation

Correlations sometimes occur between characters. These correlations can arise because of commonality, or similarity, in the underlying genotypes. The genetic cause of correlation between characters is largely due to pleiotropy, although linkage of genes on the same chromosome is a transient cause of correlation. Pleiotropy, as discussed earlier, is a property of a gene whereby it affects more than one character.

The correlations that we actually measure are the phenotypic correlations (r_p). As with variance, this correlation, or covariance, can be partitioned into its component parts. These are genetic (r_A), the correlation of the breeding values for the two traits, and environmental (r_E), which includes both environmental and non-additive genetic correlations. The genetic and environmental correlations may be quite different in magnitude and sign. If they are different in sign, it means that the genotype and the environment affect the character through different physiological mechanisms. The correlation is calculated by the appropriate covariance divided by the product of the two standard deviations of the characters which is defined by:

$$r_{XY} = \frac{Cov(X, Y)}{\sigma_X \cdot \sigma_Y} \quad (13)$$

The relative importance of r_A and r_E in determining the phenotypic correlation between two traits X and Y depends on the heritability of the two traits:

$$r_p = r_A \cdot h_X h_Y + r_E \cdot e_X e_Y \quad (14)$$

Where h is the square root of the heritability, and $e^2 = 1 - h^2$, that is the complement of heritability or the proportion of phenotypic variance that is environmental and non-additive genetic. The above equation shows that if heritability is high, then the phenotypic correlation is determined mainly by r_A , whereas the environmental correlation is more important when heritability is low.

Genetic correlations can be positive or negative and range from -1.0 to 1.0 , whereas heritability is always positive and ranges from 0.0 to 1.0 . Genetic correlations tell us how pairs of traits “covary” or change together. When genetic correlations are close to zero, different sets of genes control each trait and selection for one trait will have little effect on the other. Selection for one trait will increase the other if the genetic correlation is positive and decrease it if the genetic correlation is negative. Genetic correlations are of importance to animal breeders because they are correlations between breeding values of two traits. Correlations may be classified in three ways: strength, sign, and whether they are favorable or unfavorable. Strength of correlation is indicated by the value itself. The sign is an indication of direction of change. A negative correlation means that as one-trait increases the other decreases. A positive correlation means that the two traits tend to change in the same direction. The sign of the genetic correlation does not indicate whether the relationship between traits is favorable, only the statistical relationship. For example, the genetic correlation between feed conversion and average daily gain in pigs is negative. Because fast gains tend to be associated with low feed required per unit of gain, this illustrates a negative statistical relationship, but favorable economic relationship. A genetic correlation between traits will result in a correlated response to selection. A favorable correlation results in selection for one trait improving another. An unfavorable correlation between traits increases the difficulty of making simultaneous improvement in both traits. However, unless the correlation is very high and undesirable, both traits can be improved by selecting animals with desirable combinations of EBVs for both traits, or by proper weighting of traits in a selection index.

2.5.1. Estimation of genetic correlation

To estimate genetic correlations and covariances, one uses exactly the same mating designs as are used for estimating genetic variance and heritability, that is, offspring-parent and sibling analyses. The only differences are that more than one trait is measured and the analyses are somewhat different. For offspring-parent analysis, instead of regressing the offspring values on the parental values for the same trait, the covariance of trait X in the offspring and trait Y in the mid-parents is an estimate of $1/2$ the additive genetic covariance between the two traits. The opposite covariance is also calculated, that is, the covariance of trait Y in the offspring and trait X in the parents. This provides two estimates of the genetic correlation, which can then be averaged. The additive genetic correlation is calculated by standardizing these additive genetic covariances by the square root of the product of the two offspring-parent covariances for each trait: (Where upper case refers to the mid-parent values and lower case to the average of the offspring)

$$r_{A1} = \frac{cov(X, y)}{\sqrt{[cov(X, x)][cov(Y, y)]}} \quad (15)$$

$$r_{A2} = \frac{cov(x, Y)}{\sqrt{[cov(X, x)][cov(Y, y)]}} \quad (16)$$

When using full or half sibling data, ANOVA can estimate covariance components as well as variance components, and the correlations can be constructed. A simpler method is to calculate the correlation of breeding values, especially when these are estimated using BLUP. Both these methods have advantages and disadvantages, and neither is clearly superior to the other. The reasons that genetic correlation is important in quantitative genetic and in breeding:

1. Use for indirect selection and predict correlated response (genetic gain). In some cases, it could be expensive to measure a trait directly. If Y is an easily observed trait that is highly correlated with X, then we can improve Y instead of X, and hope to make positive change in X in the population.
2. Develop selection indices to select for multiple traits simultaneously.
3. Determine extend of genotype-environment interaction to develop breeding strategies.
4. Understand evolutionary process of traits.

2.6. Estimated Breeding Value (EBV)

Breeding value is defined as the value of an individual as a parent. Parents transfer a random sample of their genes to their offspring. Estimated breeding value gives an estimate of the transmitting ability of the parent. Since selection is about picking parents, this measurement is important to a breeding program. An EBV is an estimate of the animal's breeding value based on information available at the time you make a selection decision – whilst it is the best estimate that can be calculated from the available information, its reliability as an estimate depends on how much (and how well recorded) was the information used to calculate it. EBVs are expressed in the same units as the recorded traits (e.g. kg) and expressed relative to a common baseline for all animals in the same evaluation. They are shown as a positive or negative difference from the average breeding value of the breed. To interpret an EBV, it should always be compared with the average breeding value of the breed and the particular herd. For example, a bull with EBV of +50kg for 600 days weight is estimated to have a genetic merit 50 kg above the breed base. The average EBVs of animals in each year usually changes because of genetic progress within the herd or the breed. Therefore, it is usually more important to know how an animal or a herd compares to current average, rather than the base. EBVs can be calculated on an across-flock basis, enabling animals in the same breed to be directly compared, if strong genetic linkage exists between flocks. EBVs can not be compared across different breeds.

Some applications of EBV that will be assisted the animal breeding target:

- A well-defined breeding objective allows breeders to define the key Estimated Breeding Values (EBVs) and appropriate index needed for their breeding program.
- Selection indices provide the livestock producer with a simple description of a breeding animal to achieve a given breeding objective.
- Estimated breeding values provide an objective measurement of a desired production characteristic to compare potential breeding stock.
- Livestock producers can use estimated breeding values to select the best animals for a desired production characteristic.
- Estimated breeding values are a form of quality assurance for the selection of breeding animals.

2.6.1. Properties of EBV

1. **Variance of EBV:** the variance of EBV is equal to the square of accuracy (also referred to as 'reliability') multiplied by true breeding value; $\sigma_{\hat{g}}^2 = r^2 \cdot \sigma_g^2$. This shows the importance of accuracy: the larger the accuracy, the larger the variance and spread of EBV of animals in the population, the better we will be able to distinguish between genetically superior and average or inferior animals, and the greater the genetic superiority of selected animals will be.
2. **Prediction error variance, PEV:** Like any prediction, EBV also have a prediction error, which is the deviation of true BV from the EBV: $\varepsilon_i = g_i - \hat{g}_i$

Thus, the variance of prediction error (prediction error variance, PEV) can be defined as:

$$\sigma_{\varepsilon}^2 = (1 - r^2) \cdot \sigma_g^2 \quad (17)$$

- **Accuracy of EBV:** Defined as the correlation between the true breeding value (g_i) and the estimated breeding value (\hat{g}_i). The Accuracy of an EBV depends on how much information we have on that animal, including information on all its relatives, and on how good a picture of the genes we get using whatever measure is involved. Remember that there are three sources of information about each animal's genes. Information about the animal's performance about the trait of interest, information on correlated traits, and information from its relatives all contribute to the estimate of breeding values. The more information there is the closer the EBV will be to the true breeding value (TBV). Accuracy for EBVs can be expressed as:
- A percentage, with higher percentages meaning greater accuracy and hence the EBV is closer to the TBV.
- A standard error, which indicates the range in which the true breeding value is likely to be, and for this a smaller standard error means the EBV is closer to the true breeding value.

Accuracy Values account for the risk involved in making breeding decisions and provide buyers with the confidence that an EBV is accurate. For any trait, the accuracy of the EBV is influenced by several factors:

- Amount of information for the animal
- Amount of information from relatives
- Heritability of the trait
- Amount of information from traits correlated with the trait of interest and the strength of these correlations
- Number of animals being compared (contemporaries).

2.6.2. Methods for estimated breeding value (EBV)

Simple Regression

2.6.2.1. Own phenotypic records

The simplest form of selection is based on EBV derived from a single record of the phenotype of the individual itself. In this case, the EBV can be derived from regression of breeding value on phenotype as:

$$\hat{A}_i = b_{AP} \cdot P \quad (18)$$

This function is valid irrespective of if the phenotypic records are on the individual itself or on its relatives. The b-value will, however, be different for distinguishable sources of information. The regression of breeding value on phenotypic ($b_{A,P}$) can be derived as:

$$b_{A,P} = \frac{\text{cov}(A, P)}{\sigma_P^2} = \frac{\text{cov}(A, A + E)}{\sigma_P^2} = \frac{\text{cov}(A, A) + \text{cov}(A, E)}{\sigma_P^2} = \frac{\sigma_A^2}{\sigma_P^2} = h^2 \quad (19)$$

What we observe from equation above is that the regression of breeding value on phenotypic deviation is equal to the heritability. Therefore, if we know h^2 then we can use that to predict the breeding value of an individual if we know its phenotypic value.

Individual selection is based on an individual's own performance record or phenotype. Information on the individual itself, (i.e. the candidate to be evaluated for selection), is commonly used, when the trait can be measured on the individual directly or indirectly. Sometimes this is not possible, for example, traits that are sex-limited like milk production or female fertility can not be measured in male animals. Traits like carcass composition and meat quality can not be measured on live animals, unless an indirect method can be used (e.g. ultra-sonic measurement of carcass composition). Use of records on the individual itself is called performance testing. Also known as performance testing, it is usually optimal for traits with high heritability but only when records are expressed by both sexes. Its use may lead to maximum genetic gain through a high accuracy of evaluation and short generation interval, although it may be subject to management bias. A performance testing must be adjusted for management levels to avoid apparent phenotypic superiorities arising from better treatment rather than greater genetic value. Individual selection is usually needed for the improvement of growth, feed efficiency, and carcass traits (estimated in vivo) that can usually be measured before puberty and have moderate to high heritability (i.e., more than

20 percent). This is particularly the case for meat strains of poultry with no pedigree recording, and for goats and beef cattle with few sibs.

2.7. Relative's records

The simple regression methods for estimation of breeding value described in the previous section for own records can be extended to one or more records on a single type of relatives. Imagine a situation where one record is collected on each of m relatives of individual i for which we want to estimate the breeding value. Each relative j has the same additive genetic relationship a_{ij} with individual j .

$$\hat{A}_i = b_{A\bar{P}} \cdot \bar{P}_i \quad (20)$$

Where $\bar{P}_i = \sum_{j=1}^m x_{ij} / m$ and $b_{A\bar{P}} = a_{ij} \frac{mh^2}{(m-1)t + 1}$

Information on ancestors, collateral relatives, and the progeny test are also valuable aids to individual selection for specific traits. Several factors influence which sources of information to use when predicting breeding values for a trait, what information is available, the heritability of the trait, and how and on what individuals the trait can be measured. In genetic evaluation in practice, it is common to combine information from several sources.

- Using phenotypic records on progenies is generally the most accurate source of information for genetic evaluation. The average phenotypic value of a progeny group gives a good indication of the additive genetic effect (i.e. the breeding value) of the candidate. Progeny testing is usually indicated for selection of males when the trait is not measured in males. For example, selection for sex-limited traits such as milk production in dairy bulls will be based on progeny records. Progeny testing is not usually advised for evaluation of females, although for some traits progeny records actually measure the female's performance. For example, the weaning weight of her calf is an indication of a beef cow's milk production. The application of progeny test in the selection of females is definitely limited because of the inability to obtain many progeny from females. Progeny testing is useful also when the heritability is low and can be utilized even for traits with a heritability below 0.1, assuming the candidate has a large number of progenies (around 100-150). While a progeny test can provide an extremely accurate appraisal of an animal's breeding value, its major limitation is in the time and expense required to obtain the information.
- Phenotypic records basis of sib information (half sibs and full sibs) are often used in addition to other information, or to give supplementary information. Sib testing is applied to some traits that can not be measured on the animals that are to be used as parents and selection can only be based on the values of relatives. Sib selection may also be advised for such traits as carcass measurements, which can not be obtained on the live animal. The accuracy of sib testing depends on the number of sibs that have records. Full sibs are usually raised in the same herd; they have a common

environmental effect. This may cause a bias when they are used for prediction of breeding values, unless we are able to adjust for it.

- Information on pedigree (records from ancestors) is generally available even before the candidate is born, and can give very early information. Pedigree information provides added accuracy in female evaluations, especially in evaluating traits with low heritability. In pigs, for example, pedigree records and information from a number of relatives (e.g., sibs) are often combined as a family index.

As already mentioned, all information available is usually utilized when an animal's breeding value is predicted. The weight given to a specific source of information depends on the additive genetic relationship with the candidate, the heritability, and the amount of information (i.e. the number of progenies or sibs, etc).

Multiple Regression (Selection Index)

The selection index is a method for estimating the breeding value of an animal combining all information available on the animal and its relatives. It is the best linear prediction of an individual breeding value. When records are available from multiple sources, e.g. records on the animal itself, its dam, half sibs, progeny, etc., it will obviously be most beneficial to use all records to estimate the breeding value. This can be achieved by extending the simple regression methods described in the previous to a multiple regression setting:

$$I_i = \hat{a}_i = b_1x_1 + b_2x_2 + \dots + b_mx_m \quad (21)$$

where x_i represents the i^{th} source of records, which could be an individual record or the mean of records on a given type of relative, and b_i are partial regression coefficients. Equation above is called a selection index and the coefficients b_i are called index weights. The determination of the appropriate weights for the several sources of information is the main concern of the selection index procedure. In the above equation, the index is an estimate of the true breeding value of animal i . Properties of a selection index are:

3. It minimizes the average square prediction error, that is, it minimizes the average of all $(a_i - \hat{a}_i)^2$.
4. It maximizes the correlation ($r_{a,\hat{a}}$) between the true breeding value and the index. The correlation is often called the accuracy of prediction.
5. The probability of correctly ranking pairs of animals on their breeding value is maximized.

An assumption in the use of selection indexes to estimate breeding values is either that there are no fixed effects in the data used, or that fixed effects are known without error. This may be true in some situations. An example are some forms of selection in egg-laying poultry where all birds are hatched in one or two very large groups and reared and recorded together in single locations. But in most cases, fixed effects are important and not known without error. For example, with pigs, different litters are born at different times of the year, often in several different locations. In progeny testing schemes in dairy cattle, cows are born continuously and begin milking at different times of year and in a very large number of different herds.

In statistical terms, a breeding value predicted through selection index theory is BLP (Best Linear Prediction), but it is not guaranteed to be unbiased. The main reason to learn about selection index is that this theory provides a simple way to calculate the accuracy of selection before setting up a breeding program. This is very useful for comparing alternative strategies. For selection index theory, you do not need data. You only need to know the expected structure of the data, which sources of information that are planned to be used in the genetic evaluation. For example, using selection theory is comparing to expect precision in selecting pigs on measures of growth rate or comparing how the precision would change if heritability increases. Another reason for learning about selection index theory is that it provides a very useful framework when you want to improve several traits at the same time, by ensuring that you put the correct relative weighting on all traits in the selection criterion.

Best Linear Unbiased Prediction (BLUP)- Animal Model

Best Linear Unbiased Prediction (BLUP) is a statistical procedure that allows breeders to make better use of information than previously discussed methods of estimating genetic merit. Genetic evaluation in practice is often based on methods of BLUP, which is a linear mixed model methodology which simultaneously estimates random genetic effects while accounting for fixed effects in the data in an optimum way. Relationships among animals can be included in the model. A sire model would account for relationships through the sire (i.e. half-sibs). A sire and dam model accounts for relationships through both the sire and the dam (i.e. full and half-sibs). An animal model accounts for all relationships among all animals in the data set. It should, however, be noted that the genetic evaluation is based on phenotypic observations, and regardless of how splendid the BLUP procedure may be, it can not compensate for bad data. So, a good recording is necessary for a reliable genetic evaluation and subsequent genetic gain. It should also not be forgotten that BLUP as well as selection index assumes that the genetic parameters used are the true ones.

The properties of the BLUP methodology are similar to those of a selection index and the methodology reduces to selection indices when no adjustments for environmental factors are needed. The properties of BLUP are more or less incorporated in the name:

- Best – means it maximizes the correlation between true (a) and predicted breeding value (\hat{a}) or minimizes prediction error variance (PEV) [$var(a - \hat{a})$].
- Linear – predictors are linear functions of observations.
- Unbiased – estimation of realized values for a random variable, such as animal breeding values, and of estimable functions of fixed effects are unbiased [$E(a - \hat{a}) = 0$].
- Prediction – involves prediction of true breeding value.

In practical animal breeding, selection is often not solely on own phenotype but on estimates of breeding values (EBV) that are derived from records on the animal itself as well as its relatives BLUP for an animal model [15]. BLUP breeding values, especially from the animal model including relationship, are useful tools in selection. Selection on BLUP breeding values maximizes the probability for correct ranking of breeding animals and selection on

them maximizes genetic gain from one generation to another. Many factors contribute to this:

- The animal model makes full use of information from all relatives, which increases accuracy.
- The breeding values are adjusted for systematic environmental effects in an optimal way. This means that animals can also be compared across herds, age classes etc, assuming the data are connected.
- The procedure is flexible; various practical situations can be handled.
- Non-random mating can be accounted for.
- Several traits can be included.

Something that should be noticed is the potential risk for increased inbreeding when selection is based on breeding values including information on all relatives. The probability that several family members are selected jointly is increased, which may result in increased inbreeding. To avoid this and to optimize long-term selection response, selection on BLUP breeding values might be combined with some restriction on average relationship of the selected animals. A useful side effect of BLUP genetic evaluation is that it gives estimates of the realized genetic trend. This is achieved by comparing BLUP breeding values of animals born in different years, assuming there are connections between years through successive time overlapping or through relationships.

Genomic Selection

Most traits of economic importance in livestock are either quantitative or complex. Nevertheless, selection based on estimated breeding values, calculated from data on phenotypic performance and pedigree has been very successful. Genomic tools, such as single nucleotide polymorphism (SNP), have led to a new method of selection called “genomic selection” in which dense SNP genotypes covering the genome are used to predict the breeding value. The genetic maps are based on SNP and they enable us to divide the entire genome into thousands of relatively small chromosome segments. Then the effects of each chromosome segment are estimated simultaneously. Finally, the genomic breeding value equals the sum of all estimated chromosome segment effects. The chromosome segment effects can be estimated for a group of animals (i.e. a reference population); and for any remaining animal, only a blood or tissue sample is needed to determine its genomic breeding value. Genome-wide information allows accurate selection of young animals provided that phenotypes from sufficiently many reference animals are available. This means that genomic breeding values are especially beneficial when traditional selection is difficult such as when phenotypic recording is restricted by sex and age (e.g. very beneficial for dairy cattle). Selecting individuals based on Genomic EBV tackles three major frontiers of animal breeding: the accuracy of breeding values for traits with a low heritability, the control of inbreeding, and the generation interval.

In practice, genomic selection refers to selection decisions based on genomic estimated breeding values (GEBV). These GEBV are calculated by estimating SNP effects from

prediction equations, which are derived from a subset of animals in the population (i.e., a reference population) that have SNP genotypes and phenotypes for traits of interest. The accuracy of GEBV depends on the size of the reference population used to derive prediction equations, the heritability of the trait, and the extent of relationships between selection candidates and the reference population. Genomic selection offers many advantages with regard to improving the rate of genetic gain in dairy cattle breeding programs. The most important factors that contribute to faster genetic gain include:

- A greater accuracy of predicted genetic merit for young animals.
- A shorter generation interval because of heavier use of young, genetically superior males and females.
- An increased intensity of selection because breeders can use genomic testing to screen a larger group of potentially elite animals.

By increasing the accuracy and intensity of selection and shortening the generation interval, the rate of genetic progress for economically important traits can be approximately doubled.

3. How to approach the optimum selection in genetic program

Selection includes choosing some individuals from the population to produce more offspring than others. The decision about which animals should be selected as parents for the next generation is mainly based on assessment of breeding value of individual animals. Genetic evaluation is central to animal improvement schemes. Selecting animals based on estimated breeding value maximizes the response to selection that can be achieved. One of the most important decisions that breeders make is choosing which traits to improve in their herds. Breeders must decide among numerous traits of economic importance and determine whether to improve performance a small amount in several traits or make larger amounts of improvement in fewer traits. A selection programs will usually focus on several traits of economic importance. There are generally three methods of selection when several traits are involved [10]. Each method has strengths and weaknesses.

1. **Tandem selection:** Tandem Selection is a method by which a single trait is used as the selection criterion for one or more generations. The trait used as the selection criterion in each generation is rotated among all traits of the selection criteria in successive generations. All selection pressure is put on a single trait of interest until the performance of the herd reaches a level that the breeder desires, at which point another trait upon which to focus selection is chosen. For instance, a breeder may put all emphasis on improving marbling until a target level for percent choice is attained. At that point, the breeder realizes that performance in another trait, such as growth, needs improving and subsequently changes selection focus from marbling to growth. This method is rarely used in a strict sense because selection on one trait often produces unfavorable change in correlated traits. If there are negative correlations among traits, improvements achieved by selection for one trait in earlier generations may be cancelled out by correlated losses in subsequent generations. Tandem selection is not a recommended method of achieving maximum response to selection.

2. **Independent culling levels:** The second and likely most common method for multiple-trait selection is independent culling. With this method, a breeder chooses minimum or maximum levels for each trait that needs to be improved. Any animal not meeting all criteria is not selected for use in the breeding program. Determining the appropriate culling level for each breeder is the most difficult aspect of this method as objective methods for identification are not widely available. Another drawback of this method is that as additional traits are added, criteria for other traits likely must be relaxed in an effort to find animals that meet all criteria. One major disadvantage to both tandem selection and independent culling is that of these methods incorporate neither the costs or income resulting from production—they do not account for the economic importance of each trait, and as a result do not simplify the evaluation of potential replacements based on probable effects on profit. The foundational method for overcoming this problem and for incorporating the economics of production into selection decisions and genetic improvement was developed by Hazel (1943) and is commonly referred to as selection indexes.
3. **Selection Index:** Selection Index is a method where the net values of all traits of the selection criteria are combined into a single index value. The index is derived utilizing the heritabilities of the traits, correlation among traits, and economic value of each trait. An index value is calculated for each animal based on its performance (performance of relatives may also be included) for each trait. Selection is then based on the ranking of individuals according to index value. Selection Index has advantages over independent culling levels in that all traits are improved simultaneously and differential emphasis can be placed on each trait.

4. Optimal selection index

To optimize the design of breeding programs a full understanding of selection index theory to predict the outcome of performance recording, genetic evaluation and subsequent selection is required. The selection index theory has first been described for livestock breeders by L.N. Hazel (1943) a scientist from Iowa State University. Not much has changed the formula for selection indices Hazel developed around 60 years ago are still valid, although C.R. Henderson (1973) has shown that his mixed model equations (BLUP) are in fact Hazel's selection index, but make the calculation of selection indices computationally much easier.

When selection is applied to the improvement of the economic value of the animal, it is generally applied to several traits simultaneously [7, 10]. When these traits differ in variability, heritability, economic importance, and in the correlation among their phenotypes and genotypes, index selection has been more effective than independent culling levels or sequential selection [10, 11]. With index selection, selection is applied simultaneously to all the component traits together, with an appropriate weight being given to each trait according to its relative economic importance, its heritability and the genetic and phenotypic correlations among the different traits [20]. Therefore, with simultaneous

selection for several traits, the objective is to achieve maximum genetic progress toward a stated economic goal [6] or to improve the net merit [23], economic efficiency [5] or the aggregate breeding value of animals.

The first step in designing a livestock improvement plan is to define the breeding objective. This will determine the traits that are to be improved, their relative importance, and where change is to be directed. The breeding objective (true breeding value), which breeders are progressing, is a particular combination of weighing factors (economic weights) and EBV information of all the characters to be improved [2; 7]. The breeding objective is a list of traits that are to be improved by selection, ordered according to their relative economic values. It is aimed at improving farm income. The breeding objective depends on two major principles: 1) traits must be heritable, if selection of parents is to result in improved progeny; 2) traits must have economic value, if genetic improvement is to increase breeders' incomes.

Henderson (1963), as quoted by Harris & Newman (1994), noted that in Hazel's (1943) approach, optimum selection toward a breeding objective which defined as the sum of the n trait breeding values, each weighted by its relative economic importance:

$$\text{Breeding objective} = H = \sum_{i=1}^n a_i G_i = a_1 G_1 + a_2 G_2 + \dots + a_n G_n = v'a \quad (22)$$

where H express true breeding value, a_i economic weight for trait i , G_i breeding value for trait i . The weights a_i are usually called economic weight, but they may be based on other factors than purely economical. The last term of the equation ($v'a$) describes the equation in matrix language and v' is a row vector of economic weights and a is a column vector of true breeding values. In some literature, the breeding objective is called "aggregate genotype" because it gives a good description of breeding objective equation. When several traits are included in the breeding objective, we often want to predict a value combining all the traits, i.e. the aggregate genotype of the individual.

The breeding value (H) itself is unobservable because it contains the true breeding values, so breeding objective (H) needs to be estimated by some other function. We call this predictor the selection index or criterion that contains individual's performance that correlates best with H :

$$\text{Selection Index} = \hat{H} = I = \sum_{i=1}^n b_i X_i = b_1 X_1 + b_2 X_2 + \dots + b_n X_n = b'x \quad (23)$$

Where b_i is a selection index weight (sometimes just called b-value), X_i is a phenotypic measure. The last part of the above equation ($b'x$) expresses in matrix language where b' is a row vector of index weights and x is a column vector of phenotypic deviations. The optimum set of selection index coefficients is those which maximize the correlation (r_{HI}) or minimize the squared deviation between the selection index and the aggregate genotype (breeding objective) [25]. Hazel (1943) showed that maximum r_{HI} is achieved

when $Pb = Gv$. Selection index weights are then calculated as $b = P^{-1}Gv$, where G is a $(n \times m)$ genetic variance – covariance matrix for m traits in the breeding objective and n correlated traits in the selection index and incorporates the additive genetic relationships between sources of information; P is a $(n \times n)$ phenotypic (co)variance matrix of correlated traits in the selection index; and v is a $(m \times 1)$ vector of relative economic values in the breeding objective [4, 8]. A clear distinction should be made between the traits in the breeding objective and the characters used as selection criteria [18]. Traits that appear in the breeding objective should be those that are economically important and therefore directly linked to the costs and returns of the production situation. By contrast, the selection criteria are the characters used in the estimation of the breeding values of animals.

5. Selection index applications in livestock improvement

A selection index is a proven way to manage a lot of information simultaneously in a biologically and genetically sound manner and Selection index is one more tool for breeders to use in making selection decisions. They are predictions of the economic merit of seedstock, in the future. Thus, like every forecast, it is more appropriate to use the selection index evaluations as guidelines rather than as absolute criteria. Except for large corporate breeding organizations, it generally is not feasible for individual breeders to develop their own selection indexes, because these involve not only the relative economic weightings for component traits, but also accurate estimates of variability, heritability, and genetic and phenotypic correlation. For this reason, it is very helpful for an animal breeding enterprise to be part of a larger organization that can facilitate data recording and can compute individual breeding values for the traits considered important, using information on relationships and on the genetic parameters appropriate for the management system. A brief summary of present and potential future use of index selection approaches for several livestock species is attempted here.

5.1. Dairy cattle

The dairy industry has used selection indices to identify genetically superior sires and dams for more than 20 years. Breed associations have developed indices that are aimed somewhat more towards seedstock producers and the Animal Improvement Program Laboratory of USDA focuses their indices towards commercial dairy farms. Overtime, indices have been expanded to incorporate more traits that contribute to total lifetime merit of dairy cows. Today, selection indices available for the dairy industry have incorporated production (yield) traits, functional traits such as udder conformation, health traits, reproductive traits, calving ease, and longevity traits. Because of the huge genetic impact that individual bulls have on the dairy population, balance in selection is critical. The dairy industry has a somewhat undeserved reputation of selecting for a single trait – milk production. In truth, indices have helped our industry to evolve towards a much more balanced and comprehensive approach to selection. With selection indices, the dairy

industry has made great strides in improving functional traits like feet and leg conformation and udder conformation while continuing to improve protein and fat yields. Now that the dairy industry has genetic measures for female fertility and health/longevity traits these have been added to the indices to further broaden our definition of a balanced selection approach.

Primarily, dairy producers want cows that produce milk. However, they also want cows with sound feet and legs, cows with well-attached udders that are milked easily, cows that will stay in the herd, cows that convert milk to feed efficiently, and cows that are resistant to disease, especially mastitis. USDA will now provide an index to help them select those cows. Net Merit is an economic index that has been reported by the USDA's Animal Improvement Programs Laboratory since 1994. Net Merit (NM\$) included direct information on a sire's ability to produce longer lasting, healthier daughters by including Productive Life and SCS in the index as well a weighting for milk, fat, and protein dollars (MFP\$). Researchers have recently proposed that yield traits, health traits, and type traits should all be combined to give an estimate of lifetime profit.

Lifetime profit = milk value + salvage value + value of calves -rearing costs -feed energy - feed protein - health costs - breeding costs

This lifetime profit includes all the income and expenditures associated with production, thereby giving a good indication of a sire's net worth to the overall dairy operation. The current Net Merit expressed the advantage or disadvantage of sires in terms of dollars per 305-day lactation of their daughters.

5.2. Beef cattle

The goal of beef cattle production is to provide highly desirable beef for consumption in the most efficient manner. Knowledge of breeding, feeding, management, disease control and the beef market is fundamental to the economical production of desirable beef. The use of multi-trait selection indexes as tools for commercial cow-calf operators and seedstock breeders is rapidly evolving in the beef industry. Selection indexes are a tool, which combine Expected Progeny Differences (EPDs) for several traits into a single economic value, which can be used to make selection decisions. The difference in EPD of two bulls is the difference in expected progeny performance of their progeny, if the bulls are mated to similar cows and their progeny are in similar management and environmental conditions. EPDs are expressed in the same units as the trait. For example, Birth Weight, Weaning Weight, and Yearling Weight EPDs are in pounds, while Carcass Fat EPD is in inches. The sign of the EPD indicates direction; positive means larger (heavier weights), and negative means smaller (lighter weights). Which direction is "good" depends on the trait. Positive EPDs would be good for weaning weight but may be bad for birth weight. EPDs are valid only for comparing bulls of the same breed. Do not compare EPDs of bulls in different breeds.

The index values are interpreted like EPDs; the difference in index value between two bulls is the expected difference in average dollar value of their progeny, when the bulls are bred to similar cows. Typical beef production and economic values are used in calculating the indexes. Indexes are expressed in dollars per head, and higher indexes mean a higher dollar value per head. An index value only has meaning when it is compared to the index value of another animal of the same breed. Currently, indexes are calculated for Angus bulls.

- **Angus Weaned Calf Value (\$W):** an index value expressed in dollars per head is the expected difference in value of a bull's progeny at weaning compared to progeny of another sire. \$W accounts for differences in birth weight, weaning weight direct, maternal milk, and mature cow size.
- **Angus Feedlot Value (\$F):** an index value expressed in dollars per head is the expected difference in value of a bull's progeny for post-weaning feedlot performance compared to progeny of another sire.
- **Angus Grid Value (\$G):** an index value expressed in dollars per head is the expected difference in value of a bull's progeny when sold on a carcass grid basis compared to progeny of another sire.
- **Angus Beef Value (\$B):** an index value expressed in dollars per head is the expected difference in value of a bull's progeny for post-weaning growth performance and carcass value compared to progeny of another sire. The \$B value combines information from \$F and \$G.

A number of other breed associations also publish a variety of indexes. Each is developed to include economically relevant traits available to account for revenues and costs associated with some defined breeding situation or objective. As generalized indexes, most are based on some assumed market factors and costs that may not be completely appropriate or accurate for every production situation.

5.3. Swine

Significant improvements in economically important traits have occurred in the swine industry using economic indexes. Some of the earliest indices used in the industry were for the improvement of traits such as backfat, growth rate and feed efficiency. Selection indices were also used to improve litter size, an economically important trait, but one that could only be measured in females. With the widespread adoption of Best Linear Unbiased Prediction (BLUP) genetic evaluation procedures in the late 1980s, selection indexes could now easily include many traits that may or may not be measured on all animals. Since BLUP utilizes relationships among all animals and genetic correlations between traits, it is now possible to generate expected progeny differences (EPDs) for all traits on all animals regardless of whether the trait is recorded on each animal. This is especially appealing for sex-limited traits such as litter size or traits that cannot be measured on the live animal like meat quality.

Pig Improvement Company (PIC) has been a leader in the use of both quantitative and molecular genetics in its genetic improvement program. Prior to 1991, PIC used traditional selection index methods to improve lean yield, growth rate and feed efficiency. Best Linear Unbiased Prediction was implemented in 1991 for the three traits above plus litter size. In the mid 1990s, BLUP evaluations were expanded to include meat quality traits and other sow productivity traits. Refinements have been continued such that our current evaluation includes growth rate, feed efficiency, leanness (measured through ultrasonic backfat and muscle depth), leg soundness, reproductive traits (litter size, litter weaning weight, number of teats, still-born rate, age at first farrowing), piglet and sow mortality, meat quality traits (pH, color and marbling) and congenital defects.

The type of index used will depend upon the type of breed(s) you are raising and the intended use of your boars and gilts in commercial herds. Breeds can be grouped into three categories. Paternal or terminal breeds excel in growth rate and/or carcass traits. In commercial production, boars from paternal breeds are used to sire market hogs for terminal crosses and rotaterminal crossbreeding programs. Maternal breeds excel in litter traits and mothering ability. These breeds are used in the production of prolific replacement gilts for the terminal crosses and rotaterminal crossbreeding programs. A few breeds may fit into both the paternal and maternal categories. These dual-purpose breeds can be used in rotational crossbreeding systems. Three different selection indexes are used in swine genetic evaluation programs. The terminal sire index (TSI) is used for selection and culling in herds that have paternal or terminal breeds. This index includes only postweaning traits. The maternal line index (MLI) is used in maternal lines and dual purpose breeds for selection and culling purposes. The maternal line index includes both reproductive and postweaning traits but the reproductive traits receive twice as much economic emphasis compared to postweaning traits. The sow productivity index (SPI) ranks animals for only reproductive traits. This index is normally used for culling sows because of reproductive traits.

5.4. Poultry

Breeding for meat and egg production is an exceedingly complex process involving effective and accurate selection for numerous traits in the sire and dam lines to ensure that the final cross-bred commercial bird possesses all the required attributes. Consequently, breeding programs are very costly. The low importance of chicken breeding programs in most countries is reflected by a low proportion of breeds with a specific breeding goal and breeding strategy.

In commercial broiler breeding programs, selection addresses the following areas:

- *Feed utilization efficiency*: as feed accounts for about 70 percent of production costs, the efficiency with which birds convert feed to body weight is an important trait for direct

selection. to enable the selection of birds from the same conditions as their progeny are expected to perform in, some breeding companies have started to replace single-bird cage selection with selection of individual birds from group floor housing, using transponders on the birds and feeding stations to record food consumption.

- *Breast meat yield*: Because of the relatively high price of breast meat in developed countries, considerable efforts have been directed towards improving this trait. approaches include sib selection based on conformation and, more recently, indirect measurement technologies involving real-time ultrasound, magnetic resonance imaging, computer-assisted tomography and echography.
- *Ascites*: Breeding for rapid growth and high breast meat yield resulted in an inadequacy in the cardio-pulmonary system's capacity to oxygenate the increased blood flow associated with the increased muscle mass. This led to a significant increase in ascites in broiler flocks during the 1990s, particularly during winter. Prior to this, ascites was normally encountered only under cold, high-altitude conditions. Selection based on oximetry and plasma levels of the cardiac-derived troponin-T enzyme was demonstrated to be effective in reducing susceptibility to ascites, and commercial broiler breeders have adopted this procedure. Levels of ascites in the field are now greatly decreased, even at high altitudes.
- *Skeletal abnormalities*: The very rapid growth rate of broiler chickens encounters an enormous strain on their immature cartilaginous skeletons, resulting in high incidence of leg and skeletal abnormalities. Selection based on gait, morphology, and X-ray imaging has done much to reduce the expression of conditions such as tibial dyschondroplasia, spondylolisthesis and valgus and varus deformation in most commercial strains of broilers, but skeletal abnormalities continue to be a major focus in most breeding programs.

In commercial layer breeding programs, selection addresses the following areas:

- *Egg production and size*: genetic improvement in egg production and size is challenged by the highly canalized nature of the trait as determined by diurnal photoperiodic constraints; negative genetic correlations between egg production and early egg size; variation in the rate of increase in egg size with age; and the need to predict persistence of lay in birds selected for breeding before the third phase of production.
- *Egg quality*: shell quality is defined in terms of strength, color, shape, and texture; the first three have moderate to high heritabilities, so respond readily to selection. Shell color is determined almost exclusively by genotype, and selection is typically based on measurement using reflectance spectrophotometry. There are cultural preferences for eggs of different colors. Shell strength is a critical factor affecting profitability. Breeders have selected for improved shell strength by measuring shell thickness, specific gravity (of fresh eggs), shell deformation, and other indirect and direct parameters. Shell texture and shape aberrations and blood and meat spot inclusions are selected against by culling birds producing these eggs.

Breeding is not simply a static, intellectual pursuit, but requires a certain level of creativity and flexibility. The choices made by the individual breeders not only help to mold a strain of poultry, but they can be a source of pride and satisfaction for the effort of managing the breeding stock. Breeders should feel empowered to tailor choice of selection criteria to fit their desired goals and needs.

6. Conclusion

Improving the performance in multiple traits simultaneously is usually desired in genetic improvement programs. It is important that only traits of economic importance to the breeder and customers are included in selection objectives. Expanding the number of traits in the objective reduces the rate of improvement in individual traits but may increase overall productivity. Multi-trait improvement programs account for differences in economic value among traits, differences in heritability, variation and correlations among traits. All available information describing the performance of individuals and their relatives should be utilized. Selection indexes utilizing expected progeny deviations estimated from performance data of individuals and their relatives. Knowledge of breeding values, genetic correlations, and the relative economic importance of traits of interest is used to calculate selection indexes. Selection indexes are the best method for determining an animal's relative genetic value. Indexes exist that specifically target maternal traits, paternal traits or a desired market. Additional indexes may be developed for export verses domestic markets. Economic weights used to calculate each index would differ; however, genetic parameters are not likely to change. Breeding values and genetic correlations are population measures, which are independent of the economic value of traits. A greater understanding of genetic parameters will help producers understand and utilize genetic information.

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